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Editors

GRACE E. POTTER AND SHERIDAN BAKER

PART I. BOTANY AND FORESTRY

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PART I. BOTANY AND FORESTRY

BOTANY

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLI, 1956 (1955 Meeting)

ZYGNEMATACEAE OF WESTERN NEW YORK. I

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The algal flora of relatively few large areas of the United States is as yet adequately known. Of the many sizable areas from which algal collections are largely unreported, western New York[1] is of more than average interest, a topographically varied region which straddles a portion of the boundary between the St. Lawrence drainage basin and that of the Mississippi River. Over seven hundred algal collections were made in western New York between 1947 and 1951. The region in which these collections were made consists approximately of the eight most westerly counties of New York State (text Fig. 1) and includes what is commonly known as the Niagara Frontier area. The vascular flora has received diligent study by Zenkert (1934) and others.

Physiographically this region is a series of plains rising at successively higher levels toward the south. These plains are separated by escarpments of moderate relief, but in the southern tier of counties, where the northern limits of the Allegheny upland are found, the terrain is rugged. Although most of the region has been glaciated, the Allegany State Park area, just north of the Pennsylvania state line, is essentially or entirely driftless. The numerous streams, ponds, and swamps of this rather humid region provide abundant algal habitats.

The algal flora has proved interesting and varied, but not necessarily distinctive. To date, the larger share of the material identified belongs to species which are common or at least known from other portions of the northeastern United States. The present paper describes most of the species of *Spirogyra* which have been found here. I plan to treat other genera of the Zygnemataceae in a subsequent report. The majority of the species listed have not previously been known from New York. Determination of these species is

[1] Lists or records of algae from this area are included in Day (1882), Matthews (1932), Gordon (1934), and Blum (1951).

difficult, largely because of the great variability of certain species from one collection to another and even within one collection. An effort has hence been made here to break with the tradition of illustrating only one or two fruiting filaments, and to show in the accompanying plates much of the range in size and structure of at

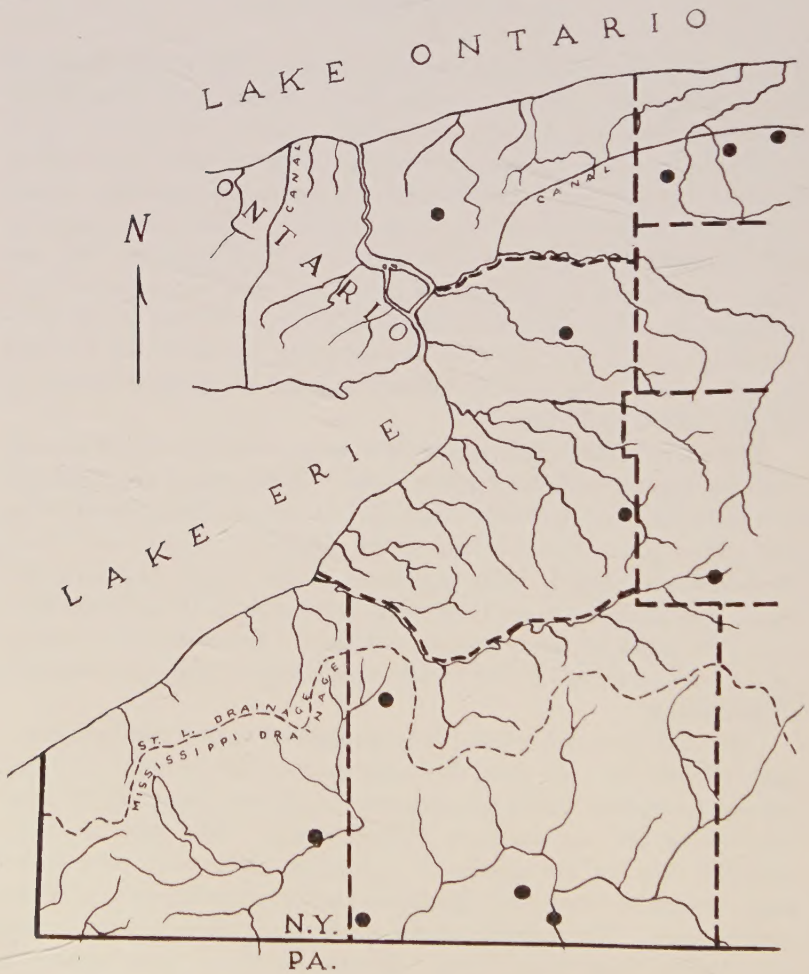

Fig. 1. Map of the western portion of New York. County boundaries are shown as heavy broken lines. Heavy dots indicate collection localities for *Spirogyra cleveana*.

least the more variable species in my collections. The nomenclature used in Transeau's *The Zygnemataceae* (1951) has been followed, and the terminology of Jao (1935) has been used with respect to spore markings and patterns.

Spirogyra catenaeformis (Hassall) Kützing

Vegetative cell diameter 20–29 μ, with plane end walls; 1 chloroplast, which makes 1–5 turns; conjugation usually lateral, rarely scalariform; conjugation tubes formed by both gametangia; fertile cells and sterile cells somewhat enlarged; zygospores ellipsoid, 29–34 $\times$ 41–82 μ; median spore wall straw-colored, smooth. (Pl. I, Figs. 1–2.)

In Scajaquada Creek, Buffalo, Erie Co., Blum 293, May 29, 1949. In springs, Lockport, Niagara Co., Blum 484, May 25, 1950.

Spirogyra varians (Hassall) Kützing

Vegetative cell diameter 27–41 μ, with plane end walls; 1 chloroplast, which makes 1–5 turns; conjugation usually scalariform, rarely lateral; conjugation tubes formed by both gametangia; fertile cells inflated on the conjugation side; some of the sterile cells inflated; zygospores variable, some ellipsoid, usually some ovoid or globose, 28–38 $\times$ 30–76 μ; median spore wall straw-colored, smooth. (Pl. I, Figs. 3–9.)

In pond, Gowanda, Erie Co., Blum 278, May 15, 1949. In swamp, Dayton, Cattaraugus Co., Blum 281, May 15, 1949. In Lake Chautauqua, Bemus Point, Chautauqua Co., Blum 497, May 30, 1950. In springs, Mendon, Monroe Co., Blum 585, Oct. 6, 1950. In ditch, West Seneca, Erie Co., Blum 673, May 14, 1951.

Spirogyra parvula (Transeau) Czurda

Vegetative cell diameter 23–25 μ, with plane end walls; 1 chloroplast, which makes 1–6 turns; conjugation scalariform in material reported here; conjugation tubes formed by both gametangia; fertile cells inflated, often separating from each other; zygospores ellipsoid, 20–27 $\times$ 40–60 μ; median spore wall thin, yellow-brown, smooth. (Pl. I, Fig. 10.)

In pond, Allegany State Park, Cattaraugus Co., Blum 503, May 30, 1950.

Spirogyra silvicola Britton

Vegetative cell diameter 37–38 μ, with plane end walls; 1 chloroplast, making 1.5–3 turns; conjugation scalariform; conjugation tubes formed by both gametangia; receptive gametangia cylindric or slightly enlarged; zygospores ellipsoid to cylindric-ovoid, 37–39 $\times$ 39–85 μ; median spore wall smooth, yellow or brown. (Pl. I, Figs. 11–12.)

In Ellicott Creek, Bowmansville, Erie Co., Blum 277, May 12, 1949.

Spirogyra teodoresci Transeau

Vegetative cell diameter 27–30 μ, with plane end walls; 1 chloroplast, which makes 2–6 turns; conjugation entirely scalariform in material reported here; conjugation tubes formed by both gametangia; fertile cells inflated on the conjugation side; zygospores ellipsoid, 24–27 $\times$ 33–65 μ; median spore wall straw-colored, smooth. (Pl. II, Figs. 1–3.)

In swamp, East Aurora, Erie Co., Blum 286, May 28, 1949.

Spirogyra longata (Vaucher) Kützing

Vegetative cell diameter 31–39 μ, with plane end walls; 1 chloroplast, making 2–5 turns; conjugation entirely scalariform in material reported here; conjugation tubes formed by both gametangia; fertile cells cylindric; zygospores ovoid or cylindric-ovoid, 33–41 $\times$ 37–77 μ; median spore wall straw-colored, smooth. (Pl. II, Figs. 4–7.)

Olean, Cattaraugus Co., coll. R. Messer, Nov., 1948. In swamp, Bethany, Genesee Co., Blum 297, June 1, 1949. In springs, Lockport, Niagara Co., Blum 484, May 25, 1950. In pond, Frewsburg, Chautauqua Co., Blum 493, May 27, 1950. In pond, Limestone, Cattaraugus Co., Blum 506, May 31, 1950.

Spirogyra porticalis (Müller) Cleve

Vegetative cell diameter 32–48 μ, with plane end walls; 1 chloroplast, making 3–5 turns; conjugation scalariform; tubes formed by both gametangia, widest at the point of fusion; fertile cells cylindric or slightly enlarged; sterile cells cylindric or slightly inflated; zygospores usually ovoid, occasionally ellipsoid or irregular in shape,

32–39 × 33–54 μ; median spore wall straw-colored and smooth. (Pl. II, Figs. 8–10.)

In pond, Eagle Harbor Station, Orleans Co., Blum 464, May 2, 1950.

Spirogyra emilianensis Bonhomme

Vegetative cell diameter 43–48 μ, with plane end walls; 4 chloroplasts in material reported here, making 0.2–2.5 turns; conjugation scalariform; conjugation tubes formed by both gametangia; fertile cells cylindric; zygospores ovoid, 48–59 × 78–93 μ; median spore wall brown, smooth. (Pl. II, Fig. 11.)

In springs, Allegany State Park, Cattaraugus Co., Blum 345, Aug. 16, 1949.

This species has been reported from Massachusetts, but the collection recorded here appears to be the only other collection from North America. The New York material is somewhat smaller than the material reported by Transeau (1951), but in other respects agrees well.

Spirogyra plena (W. & G. S. West) Czurda

Vegetative cell diameter (41) 47–54 μ, with plane end walls; 2–3 chloroplasts; conjugation scalariform; conjugation tubes wide and formed by both gametangia; fertile cells cylindric or enlarged on the conjugation side; zygospores mostly ovoid, sometimes ellipsoid or subglobose in material reported here, 44–50 × 50–102 μ; median spore wall straw-colored, smooth. (Pl. II, Fig. 12.)

In springs, Sandusky, Cattaraugus Co., Blum 332, Aug. 5, 1949.

The measurements noted here for *Spirogyra plena* somewhat exceed the size range for vegetative filaments given by Czurda (1932) and by Transeau (1951).

Spirogyra majuscula Kützing

Vegetative cell diameter 47–52 μ, with plane end walls; (3) 5–8 chloroplasts, straight or making 0.3 turn; conjugation scalariform; conjugation tubes formed by both gametangia; fertile cells shortened, cylindric or slightly inflated; zygospores lenticular, 44–50 × 52–65 μ; median spore wall brown, smooth. (Pl. III, Figs. 1–3.)

In ditch, Allegany State Park, Cattaraugus Co., Blum 63, May

30, 1948. In creek, Wesley, Cattaraugus Co., Blum 683, June 19, 1951.

Spirogyra fluviatilis Hilse

Vegetative cell diameter 29–34 μ, with plane end walls; 3–5 chloroplasts, making 1.5–3.5 turns in the cell; conjugation scalariform; conjugation tubes formed by both gametangia; fertile cells inflated; zygospores ovoid, 41–51 $\times$ 47–102 μ; median spore wall brown, grooved in an intricate pattern of corrugations. (Pl. III, Figs. 4–5.)

In Cazenovia Creek, Griffins Mills, Erie Co., Blum 219, April 1, 1949.

Spirogyra tenuissima (Hassall) Kützing

Vegetative cell diameter 13–17 μ, with replicate end walls; 1 chloroplast, which makes 3–6 turns; conjugation lateral and scalariform; conjugation tubes from both gametangia, but the portion from the male cell distinctly longer in material reported here than that from the female cell; fertile cells inflated or enlarged toward the middle; zygospores ellipsoid, 24–29 $\times$ 51–78 μ, median spore wall straw-colored, smooth. (Pl. III, Figs. 6–9.)

In pond, Gowanda, Erie Co., Blum 278, May 15, 1949. In swamp, Dayton, Cattaraugus Co., Blum 280, May 15, 1949.

The specimens described here are probably large individuals of the exceedingly variable *Spirogyra tenuissima*, although the size and the presence of relatively few inflated cells are unusual.

Spirogyra inflata (Vaucher) Kützing

Vegetative cell diameter 20–22 μ, with replicate end walls; 1 chloroplast, making 2.5–6 turns; conjugation lateral and scalariform; conjugation tubes formed by both gametangia, but mostly by the male cell; fertile cells inflated on all sides; zygospores ellipsoid, but frequently assymmetric, 26–33 $\times$ 65–78 μ, median spore wall straw-colored, smooth. (Pl. III, Figs. 10–13.)

In ditch, Pekin, Niagara Co., Blum 658, May 10, 1951.

Spirogyra spreeiana Rabenhorst

Vegetative cell diameter 20–24 μ, with replicate end walls; 1 chloroplast, making 1.5–4 turns in the cell; conjugation scalariform

only in material reported here; conjugation tube formed from both gametangia, but the portion from the male cell somewhat longer than the other; fertile cells enlarged and inflated; sterile cells not enlarged; zygospores ellipsoid, 31–37 × 61–83 μ, median spore wall straw-colored, smooth. (Pl. III, Figs. 14–15.)

In swamp, Eagle, Wyoming Co., Blum 650, April 21, 1951.

Spirogyra laxa Kützing

Vegetative cell diameter 26–34 μ, with replicate end walls; 1 chloroplast, making 3–5 turns in the cell; conjugation lateral and scalariform; conjugation tubes from both gametangia; fertile cells cylindric; zygospores ellipsoid to cylindric, 23–38 × 64–96 μ, median spore wall straw-colored, smooth. (Pl. IV, Figs. 1–3.)

In pond, Lancaster, Erie Co., Blum 283, May 21, 1949. In swamp, East Aurora, Erie Co., Blum 286, May 28, 1949. In pond, Albion, Orleans Co., Blum 489, May 25, 1950. In pond, Frewsburg, Chautauqua Co., Blum 493, May 27, 1950.

Spirogyra cleveana Transeau

Vegetative cell diameter (29) 34–41 μ, with replicate end walls; 1–2 chloroplasts, making 3–6 turns; conjugation scalariform; conjugation tubes from both gametangia; sterile cells often inflated; fertile cells cylindric or slightly enlarged; zygospores cylindric-ovoid, 34–50 × 70–125 μ, outer spore wall hyaline, of two layers, the innermost of which is hyaline and scrobiculate; median spore wall smooth, yellow. (Pl. IV, Figs. 4–5.)

In swamp, Clarence, Erie Co., Blum 271, May 12, 1949. In swamp, Dayton, Cattaraugus Co., Blum 281, May 15, 1949. In pond, Eagle Harbor Station, Orleans Co., Blum 464, May 2, 1950. In millrace, Shelby, Orleans Co., Blum 487, May 25, 1950. In pond, Albion, Orleans Co., Blum 489, May 25, 1950. In pond, Ellington, Chautauqua Co., Blum 494, May 27, 1950. In ditch, Allegany State Park, Cattaraugus Co., Blum 496, May 30, 1950. In pond, Allegany State Park, Cattaraugus Co., Blum 502, May 30, 1950. In pond, Strykersville, Wyoming Co., Blum 648, April 21, 1951. In swamp, Eagle, Wyoming Co., Blum 650, April 21, 1951. In ditch, Pekin, Niagara Co., Blum 662, May 10, 1951.

This species is by far the commonest fruiting *Spirogyra* in my

collections, and has been found throughout the range covered (text Fig. 1), in drainage regions of both the St. Lawrence and the Mississippi rivers. It is usually present in these collections in small quantities and mixed with other algae. The high level of frequency in western New York is probably a somewhat local phenomenon, for no mention of such high frequency has been accorded this species in other works on the North American flora.

Spirogyra rugosa (Transeau) Czurda

Vegetative cell diameter (9.5) 11–14 (17) μ, with replicate end walls; 1 chloroplast, making 2–6 turns in the cell; conjugation lateral and scalariform; conjugation tube formed by both gametangia, but mostly by the male cell; fertile cells inflated toward the middle; zygospores ellipsoid, 24–33 $\times$ 54–85 μ; median spore wall yellow-brown, minutely scrobiculate with angled pits, the walls surrounding which form a reticulum in certain specimens. (Pl. IV, Figs. 6–11.)

In swamp in Genesee Co., near Alden, Blum 239, April 20, 1949. In swamp, Clarence, Erie Co., Blum 274, May 12, 1949. In ditch, Pekin, Niagara Co., Blum 658, May 10, 1951.

Spirogyra inconstans Collins

Vegetative cell diameter 20–37 μ, with replicate end walls; 2–3 chloroplasts, making 0.5–1.5 turns in the cell; conjugation scalariform and lateral; conjugation tubes formed from both gametangia; gametangia reflexed, usually not more than one or two consecutive gametangia in a series; fertile cell inflated; zygospores ellipsoid, 41–49 $\times$ 85–130 μ; median spore wall brown, reticulate-aculeate. (Pl. IV, Figs. 12–14.)

In pond, Albion, Orleans Co., Blum 486, May 2, 1950.

Spirogyra tetrapla Transeau

Vegetative cell diameter 28–31 μ and 41–44 μ, with replicate end walls; 1–3 chloroplasts, making 2–8 turns in the cell; conjugation scalariform; conjugation tubes formed by both gametangia; fertile cells enlarged or inflated; zygospores ellipsoid or ovoid, 34–47 $\times$ 57–112 μ, median spore wall of two layers, of which the outer is thin and irregularly corrugate, the inner finely reticulate, yellow. (Pl. IV, Figs. 15–16.)

In swamp, Dayton, Cattaraugus Co., Blum 280, May 15, 1949.

In pond, Onoville Station, Cattaraugus Co., Blum 500, May 30, 1950.

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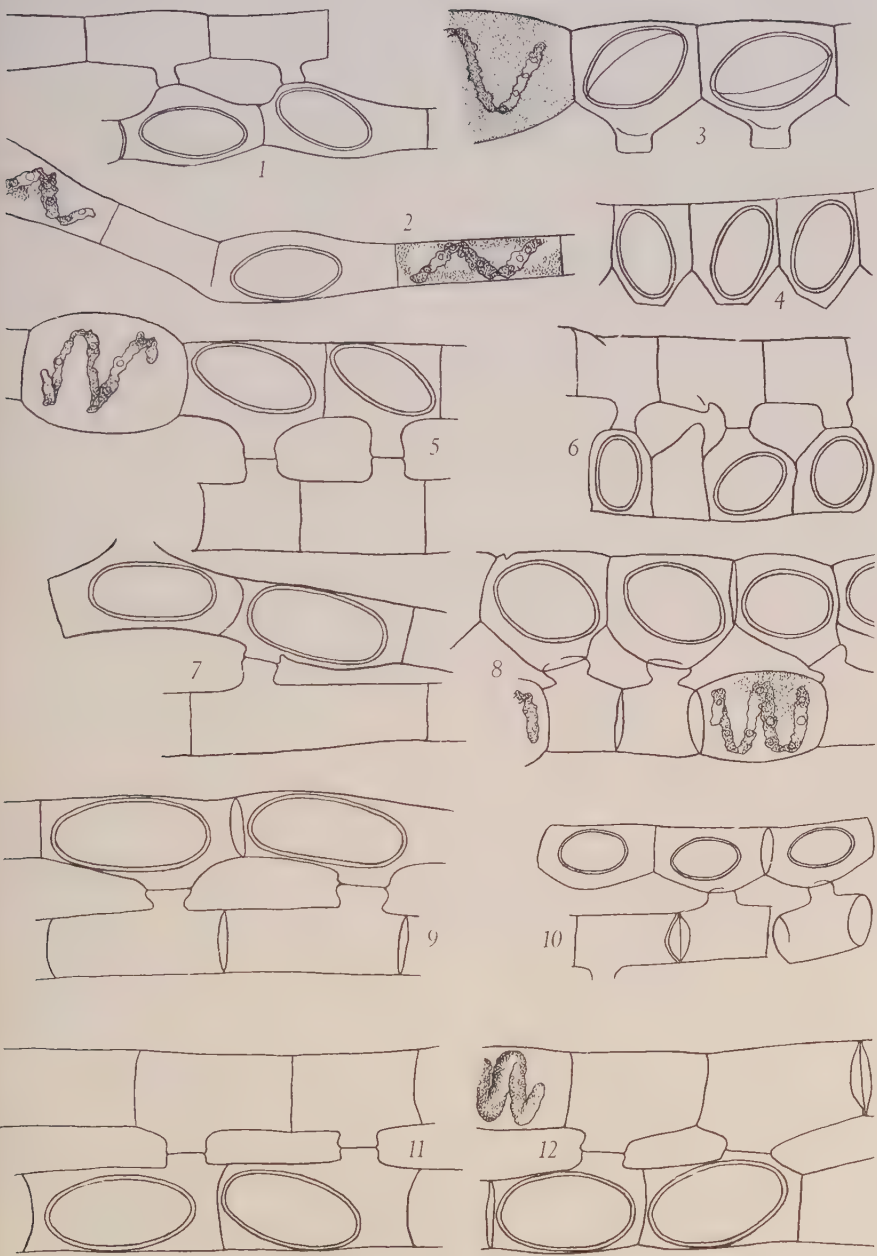
EXPLANATION OF PLATE I

FIGS. 1–2. *Spirogyra catenaeformis.* × 250

FIGS. 3–9. *S. varians.* Note the great variation in the shape of the zygospore and of the receptive (female) gametangium. × 250

FIG. 10. *S. parvula.* × 250

FIGS. 11–12. *S. silvicola.* × 250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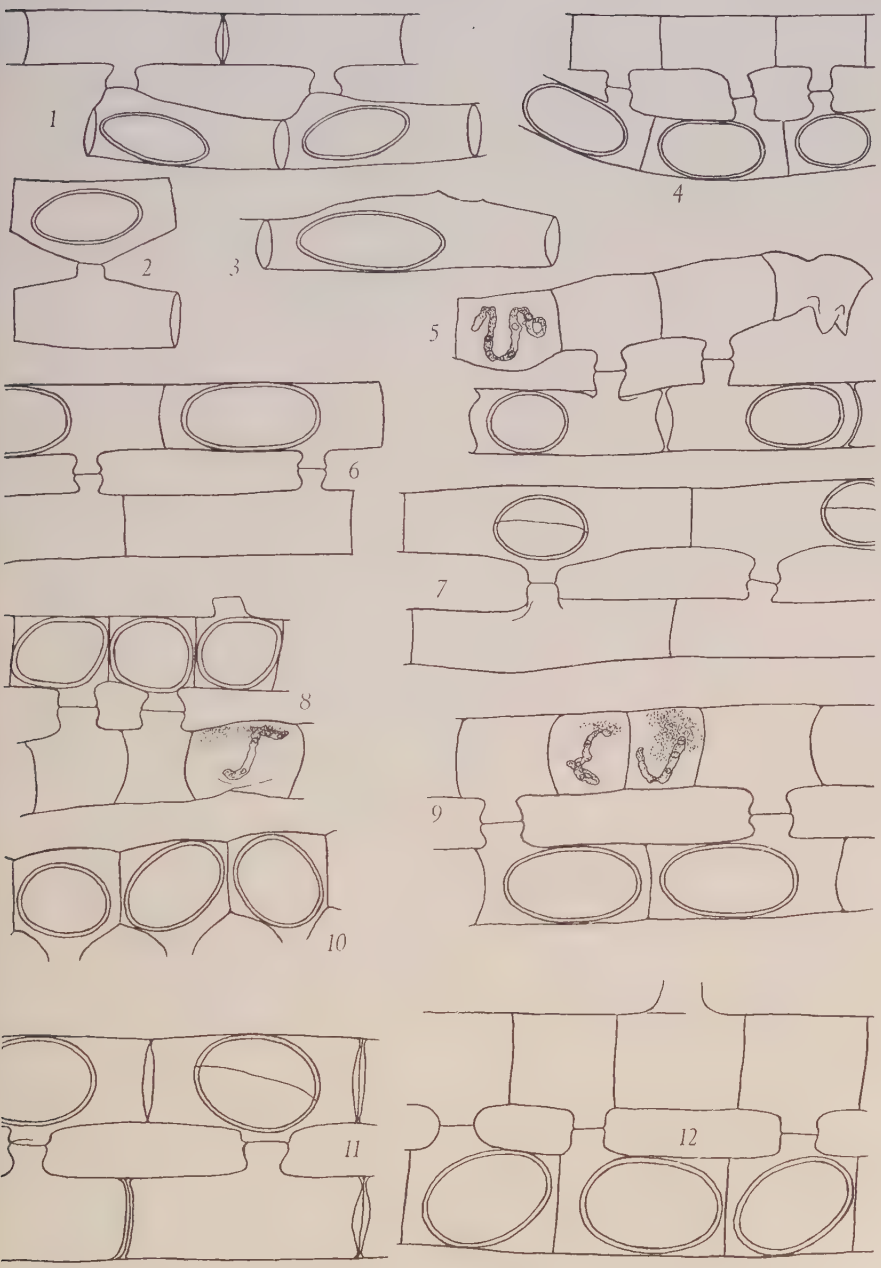
EXPLANATION OF PLATE II

FIGS. 1–3. *Spirogyra teodoresci.* × 250
FIGS. 4–7. *S. longata.* × 250
FIGS. 8–10. *S. porticalis.* × 250
FIG. 11. *S. emilianensis.* × 250
FIG. 12. *S. plena.* × 250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EXPLANATION OF PLATE III

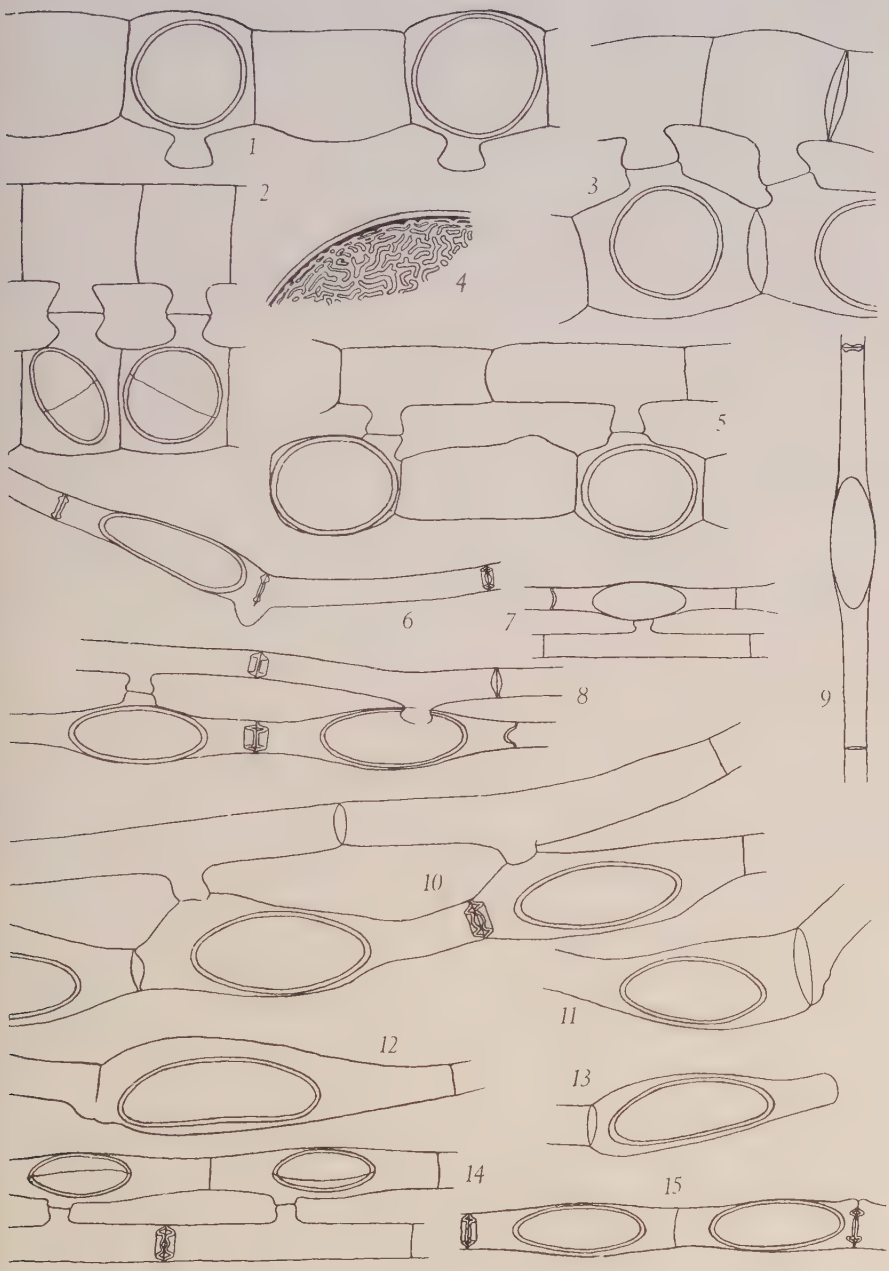
FIGS. 1–3. *Spirogyra majuscula.* × 250

FIGS. 4–5. *S. fluviatilis.* Figure 4 shows a portion of the zygospore wall; × 1000. Figure 5, × 250

FIGS. 6–9. *S. tenuissima.* × 250

FIGS. 10–13. *S. inflata.* × 250

FIGS. 14–15. *S. spreeiana.* × 250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EXPLANATION OF PLATE IV

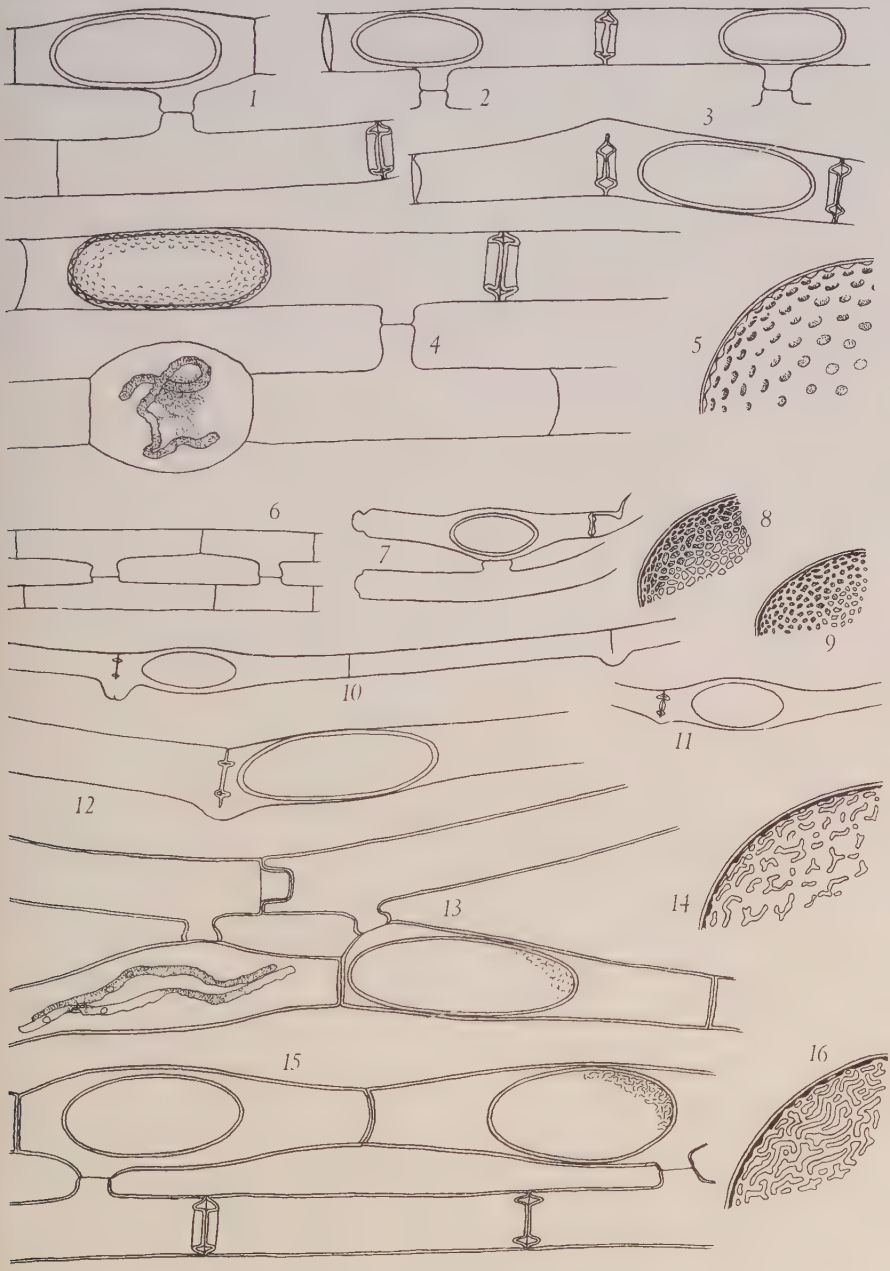
FIGS. 1–3. *Spirogyra laxa.* × 250

FIGS. 4–5. *S. cleveana.* Figure 4, × 250. Figure 5 shows a portion of the zygospore wall; × 1,000

FIGS. 6–11. *S. rugosa.* Figures 6–7, × 250. Figures 8–9 show a portion of the wall of different zygospores; note the variability in the shape and spacing of the pits; × 1,000

FIGS. 12–14. *S. inconstans.* Figures 12–13, × 250. Figure 14 shows a portion of the zygospore wall; × 1,000

FIGS. 15–16. S. tetrapla. Figure 15, × 250. Figure 16 shows a portion of the zygospore wall; × 1,000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Papers of the Michigan Academy of Science, Arts, and Letters
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THE IDENTITY OF *POLYPORUS TRABEUS* ROSTK.

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Sessile species of *Polyporus* with soft, white context are generally common in the flora of the North Temperate Zone, and their identification offers particularly difficult taxonomic problems. The microscopic details, required for their determination, were rarely given in the original descriptions, and type or authentic specimens usually no longer exist. The identity of such plants depends on the necessarily uncertain basis of a continuing tradition or on an interpretation of the original description. *Polyporus trabeus* Rostk. is an example in point.

The most common interpretation of this species, which was well described and illustrated by Rostkovius (1838, p. 59 and pl. 28), is that it is a member of the *Polyporus lacteus* Fries–*P. albellus* Peck–*P. chioneus* Fries complex, in which the sporophores are typically sessile and convex, with soft, white, mild context, slender allantoid spores, and without sterile hymenial structures. This is the concept held by Lloyd (1915, p. 301), Pilát (1936–42, p. 187), Bondarzew (1953, p. 190), and Donk (1933, p. 150). The concept is a very reasonable one, since it agrees with the original description and since this complex of species is a common element in the Central European flora.

A wholly different concept of Rostkovius' species was proposed by Bresadola (1908, p. 37), who so identified a collection from France sent to him by Bourdot (Bourdot No. 3806). His interpretation was followed by Bourdot and Galzin (1927, pp. 541–542), as is demonstrated by the eighty-one packets so named in the Bourdot collection in Paris. The fruiting body, as described by Bourdot and Galzin, varies from usually resupinate or effused-reflexed to rather

rarely sessile, often transversely elongated, white to pale yellowish- or reddish-brown, with tubes up to 10 mm. long and pores 0.1–0.6 mm. wide, averaging 3–4 per mm.; context becoming fragile, friable; spores cylindrical, straight or slightly curved, 4.5–6 × 1–1.75 μ.

The Bourdot and Galzin description may be amplified. Lundell finds the species in several localities in Sweden. It was best developed at Femsjö, the birthplace and principal collecting ground of Elias Fries, who probably had not distinguished this species from *Polyporus fragilis* Fries. It is strikingly similar (see Pl. I, Fig. 1) to that species and closely allied to it. The pore surface does not change to rusty brown on being touched, as in *P. fragilis*, but remains unaltered. On drying it does not darken, and it becomes fragile and almost chalky. Lowe, by study of about one hundred collections, establishes that the context, though usually fragile and friable in dried collections, may be in part waxy and quite firm, as it is in Bourdot Nos. 3806 and 17619, in Lundell No. 1645, and in others. The context hyphae are clamped, 2–4 (5) μ in diameter. The spores may vary somewhat more, being 4–8 × 1.5–2 μ as Lowe measures them. Additional characteristics are the taste, which is usually intensely bitter, or occasionally tardily bitter, or, quite rarely, almost mild, and the regular presence of hyphal pegs (Pl. I, Fig. 3) along the hymenium.

The characteristics given above do not sharply distinguish this species from some others of similar habit and structure. No unique and diagnostic structure has ever been published—or observed, so far as herbarium notes, with one exception, indicate. Such a feature exists, however. Gloeocystidia, both hymenial and tramal in origin, are frequently abundant and conspicuous, varying from 5 μ to 11 μ in diameter and projecting up to 20 μ beyond the hymenium. These are sometimes thick-walled in the lower portion and hyaline (Pl. I, Fig. 2*c*), closely resembling cystidia as illustrated by Weresub (1953); or they may have a more or less brown color and grade into a thin-walled, colored, typical gloeocystidium (Pl. I, Fig. 2*g*). Most gloeocystidia resemble in shape and position the one on the right in our Figure 2*g*, but they may vary from a cylindrical type extending well above the basidia to ones having as wide a diameter as that shown in the gloeocystidium at the left in the same figure. The identity of these hymenial structures has been kindly confirmed by

D. P. Rogers. So far as is known, gloeocystidia are found among the polypores only in this species.

Gloeocystidia may vary greatly in abundance. In some collections they were found only after repeated sectioning of ample material. Noncystidiate specimens which agree in every other characteristic with the Bourdot collections would be referred by us to *Polyporus subsericeomollis* Romell, in which we have not found these structures. In one of his specimens of *P. subsericeomollis* (No. 12605), however, Romell apparently observed them, for his notes say "Cyst. obtuse fusiform. 20 × 5 μ." Lowe was unable to repeat the observation. A sample sent by Romell to Bourdot (Bourdot No. 24499, apparently a segregate from Romell No. 12605) was identified by Bourdot as *P. trabeus*.

In the opinion of Lundell, *Polyporus trabeus* and *P. subsericeomollis* cannot be synonymous, for the characteristic gloeocystidia have not been found in Romell's material. Lowe, on the other hand, considers that these plants are the same species, and that Romell's material is merely an acystidiate condition of a variable species. It should be noted that Romell's material is very scanty, and that extensive sectioning cannot be done.

Polyporus undosus Peck is somewhat similar, and Pilát (1936–42, p. 189) has so referred the Bourdot and Galzin concept of this plant. *Polyporus undosus* is quite distinct, however, in having a mild taste, larger pores (1–2 per mm.), and larger hyphae, 5–8 μ in diameter. *Polyporus stipticus* Fries, as illustrated in *Icones selectae Hymenomycetum* (1877–84, p. 80 and pl. 181, fig. 2), almost exactly matches the specimen here illustrated (Pl. I, Fig. 1), but that name is now applied in European mycology to quite a different plant, the same as *P. immitis* Peck of American mycology. Lowe confused resupinate specimens of this with *Poria notata* Overh., and his records (1946, p. 70) of *Poria notata* on coniferous substrata in New York apply instead to *Polyporus trabeus*.

The wide distribution and relative abundance of this fungus make it rather certain that it has been placed under other names. For that reason, a revision of the nomenclature of the species is postponed until an extensive survey of allied species can be made.

Lowe was supported in part in this work by funds from the National Science Foundation. We both acknowledge with thanks the

privilege of studying specimens from the following herbaria: Muséum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris, France (institutional designation—PC); Botaniska Museet, Uppsala Universitet, Sweden (UPS); Herbarium, Royal Botanic Gardens, Kew, England (K); and Naturhistoriska Riksmuseet, Stockholm, Sweden (S). Specimens seen were collected in the following countries and are now in the herbaria designated: in Europe, from Austria (S, PC), Denmark (K), England (PC), France (PC), Germany (S), Poland (PC), Sweden (S, UPS); and in North America, from Manitoba (Department of Agriculture, Ottawa), Michigan (University of Michigan Herbarium), New York (National Fungus Collections, Beltsville, Md.; New York Botanical Garden, New York, N. Y.), and Pennsylvania (Pennsylvania State University, University Park, Pa.).

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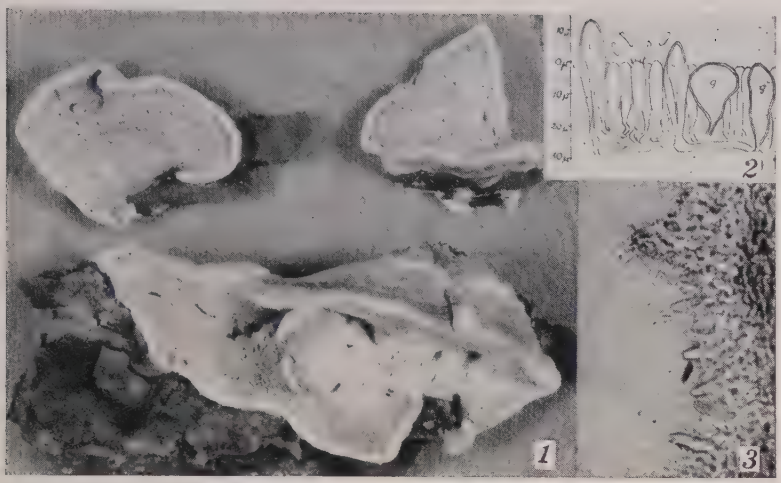

Features of an unusually well-developed specimen of *Polyporus trabeus*, Lundell No. 1645

FIG. 1. Habit. × 1

FIG. 2. Hymenial structures. Cystidia-like (*c*) and more typical gloeocystidia (*g*) are shown.

FIG. 3. Photomicrograph of the hymenium, showing gloeocystidia and a hyphal peg. × 270

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RESPONSE OF *GLOMERELLA* CONIDIA TO IRRADIATION BY X-RAYS AND FAST NEUTRONS*

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Living organisms are being exposed to increasing doses of ionizing radiations of various types. It is of growing importance, therefore, to understand the mechanisms by which ionizing radiations produce biological effects. These effects, though perhaps attributable to a common basic radiochemical action, may be divided into two classes: (1) the physiological effects, which are of significance to the irradiated organism, and (2) the genetic effects, which, though more subtle than the immediate physiological ones, are frequently no less damaging to the descendants of the irradiated organism.

The best evidence to date (Spencer and Stern, 1948) suggests that no threshold dose of radiation exists for the production of genetic effects. Even minute doses of radiation which cause no physiological injury nevertheless induce deleterious genetic changes. The large variety of radiations now abundantly available exhibit diverse characteristics, both as measured physically and as measured biologically, and a detailed examination of the differences in radiobiological effect of these various types of ionizing radiation may help to clarify the basic mechanisms by which energy of radiation absorbed in tissue produces biological damage. This report is concerned with the lethal and mutagenic characteristics of X-rays and fast neutrons on the cells of the fungus *Glomerella*.

Materials and Methods

Glomerella is an ascomycete (see Wheeler, 1950, and Markert and Owen, 1954, for references to previous work with *Glomerella*) with

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simple, defined nutritional requirements; the wild type will grow either in a liquid medium or on a solid agar medium containing only inorganic salts and an organic source of energy such as sucrose. The fungus is easily cultured in the laboratory and, on an appropriate medium (Westergaard and Mitchell, 1947), produces abundant uninucleate haploid conidia. These conidia are covered by a soluble, slightly sticky substance that apparently prevents germination and retards desiccation. The spores adhere in clumps to each other and to the culture medium and thus are not readily airborne and do not contaminate the laboratory. No multinucleate conidia have been observed. After germination on a minimal or complete agar medium (see Markert, 1950, for media), these uninucleate conidia produce small colonies, which in petri-dish cultures may be easily counted and then transferred to culture-tube agar slants. The growth rate of *Glomerella* is convenient for laboratory manipulation. About thirty to thirty-six hours at 25° C. suffice for germination of conidia and formation of colonies which are of sufficient size to be counted readily or transferred to agar slants. After an additional four or five days of growth on agar slants the colony is large enough and has adequate differentiation to permit a final evaluation of its visible hereditary characteristics.

A genetic analysis of mutant colonies may be made after crossing complementary sexual types (Markert, 1949) by plating out ascospores from crushed perithecia and picking colonies at random or by isolating single spores from individual asci, as is commonly done with *Neurospora*. However, since the average size of ascospores is about $23 \times 5\ \mu$, the isolation of individual spores is a difficult task without the aid of a micromanipulator.

The genetic analysis of individual mutants is inevitably a very time-consuming task. Crossing and the formation of mature ascospores take from one to two weeks, after which at least eight more days are required to make the genetic analysis of any individual mutant.

The lethal effects of radiation on conidia may, of course, be measured by determining the fraction of the conidia which are able to germinate and to form colonies when plated out in a suitable medium. Preliminary determinations of spore concentrations may be made by counting the spores in an aliquot of the suspension with the aid of a hemocytometer. By ascertaining the proportion of

visible mutants among the surviving colonies a measurement of the mutagenic effect of the radiation may also be obtained.

The fungus mycelium, which grows as a dense feltlike mat on the surface of an agar culture medium, is a sensitive reflector of genetic change. Genetic changes are indicated by variations in pigmentation, morphology, or growth rate. Pigmentation may vary from white through various shades of gray to black, with red, orange, yellow, brown, and even greenish hues added in genetically determined amounts. A multitude of distinct morphological variants may be recognized, and variations in growth rate of about 10 per cent or more can be satisfactorily determined. The mutability is such that at appropriate doses of irradiation more than 50 per cent of the surviving colonies may be recognized as mutant. Mutations affecting biochemical synthetic ability also occur, and these mutants likewise exhibit a changed appearance on complete medium. Specific growth requirements may be determined by the same general methods used with *Neurospora* (Beadle, 1945). Although liquid media have frequently been used, solid media are better for revealing partial reductions in ability to synthesize given metabolites.

Most of the labor and time consumed in working with *Glomerella* is spent in the transfer of colonies from petri dishes to culture tubes (18 × 150 mm., containing 6 ml. of complete agar medium). This step is essential if mutants are to be identified. Furthermore, it is important to pick all the colonies that develop on any plate, since the late-germinating spores produce a higher percentage of mutants than do the early-germinating spores, in contrast with the results obtained with *Neurospora* (Sansome *et al.*, 1945). With some practice, a skillful person can transfer more than 120 colonies an hour from petri dishes to culture tubes. Thus data of statistical significance can be obtained within a relatively short time. In the experiments reported here, colonies were picked from each plate on both the second and the third day following the plating out of irradiated spores. By the end of the third day all but a negligible fraction of the viable spores had germinated; the few that germinated later were ignored.

One restrictive characteristic of *Glomerella* stems from the fact that the conidia do not survive lyophilization. Therefore all spores must be irradiated in liquid suspension or on the culture medium where sporulation occurs and where the spores are protected from

death by desiccation. In a distilled-water suspension a very few spores will have visibly germinated within five hours, and chromosome division may have occurred some time previously, although the nucleus itself does not generally divide during the early stages of germination. Consequently, a suspension of spores should be exposed to irradiation within three or four hours of the time the suspension is made, and plated out within a few hours to prevent entanglement of growing hyphae. If more time is required, then the spores must be irradiated on the sporulated mycelium, where both germination and desiccation are inhibited. Spores have been satisfactorily tested for radiation effects as long as fourteen weeks after irradiation of culture tubes containing a nongrowing sporulated mycelium.

The auspicious characteristics of *Glomerella* for the study of radiation effects prompted a series of experiments to measure the response of *Glomerella* conidia to irradiation over a wide range of dosage by ultraviolet light (Markert, 1953), X-rays, and fast neutrons. Only the effects of the ionizing radiations will be presented in this paper.

A source of X-rays was provided by a Westinghouse industrial X-ray unit with a Machlett thermax tube operated at 120 kilovolts and 8 milliamps. The output in roentgens as measured by a Victoreen chamber at a distance of 15 cm. from the target with no shielding was 602 r per minute. In the irradiations reported here a 1 ml. suspension of conidia was placed in a small beaker in the X-ray beam 9 cm. from the target. Since the radiation received at any given distance from the target varies approximately inversely as the square of the distance, the dose received at 9 cm. must have been about 1,670 r per minute, although increased soft radiation close to the target probably makes this figure somewhat too low. The spectrum of wave lengths emitted was not measured, but probably ranged from about 0.1 Å. (Lea, 1947) to much longer wave lengths, since no shielding was used to remove the softer radiation. The wave length emitted at greatest intensity was probably about 0.2 Å. All X-radiations were conducted at a distance of 9 cm., and the total dose for each irradiation was set by the duration of exposure. Exposures between 6 minutes and 120 minutes were employed, thus giving a range of X-ray dosage from approximately 10,000 r to 200,000 r. Although relative dosages are reasonably

exact, the absolute dose in international roentgens may be in error as much as 10 per cent.

Fast-neutron irradiation was provided by the nuclear reactor at Oak Ridge, Tennessee. Dosage of fast neutrons as measured by a Victoreen thimble chamber was varied between 27,670 rep and 133,000 rep. There was also a gamma-ray contamination of from 5 per cent to 10 per cent that was not included in the listed neutron doses. In contrast to the use of a suspension of spores in distilled water for the X-radiation, the entire culture tube containing a

TABLE I

MUTATION OF GLOMERELLA CONIDIA AT VARIOUS DOSAGES OF X-RADIATION

Dose in roentgens	Colonies examined	Number of mutants	Percentage of mutants	Probable error
10,000	332	6	1.8	±0.5
20,000	350	20	5.7	±0.8
30,000	333	33	9.9	±1.1
40,000	302	33	10.9	±1.2
50,000	447	52	11.6	±1.0
60,000	276	42	15.2	±1.5
80,000	532	144	27.0	±1.3
100,000	443	144	32.5	±1.5
125,000	393	127	32.3	±1.6
150,000	352	125	35.5	±1.7
175,000	318	118	37.1	±1.8
200,000	142	60	42.2	±2.8

sporulated mycelium of *Glomerella* was exposed to the neutron bombardment. After irradiation, spore suspensions were made, counted with the aid of a hemocytometer, and plated out. The percentage of viable spores was determined by calculation from colony counts on the dilution plates. Lethal effects of the neutrons were calculated by comparison with the percentage of viable spores in a control tube of the same age which had not been irradiated. A control of this kind is not so satisfactory as an aliquot taken from a spore suspension which is then irradiated, since culture tubes that are several weeks old do not always contain the same percentage of viable spores, presumably because of the cumulative effect of minor differences in environmental conditions to which the tubes have been subjected.

Results

Both the lethal and the mutagenic effects of each type of radiation were measured. The data are recorded in Tables I, II, and III. The killing effect of neutron bombardment and of X-radiation

TABLE II

Relationship between Dosage and the Mutagenic and Lethal Effects of Fast Neutron Bombardment on Glomerella Conidia

Dose in rep	Logarithm of survivors per million	Number of colonies examined	Number of mutants	Percentage of mutants	Probable error
27,670	5.73	629	68	10.8	±0.8
54,000	5.39	655	95	14.5	±0.9
67,650	5.27	611	139	22.7	±1.1
87,510	5.03	795	247	31.0	±1.1
100,000	4.85	817	333	40.8	±1.2
133,000	4.58	132	69	52.3	±2.9

TABLE III

Relationship between the Mutagenic and Lethal Effects of X-radiation on Glomerella Conidia

Logarithm of survivors per million	Number of colonies examined	Number of mutants	Percentage of mutants	Probable error
5.83	332	6	1.8	±0.5
5.58	471	32	6.8	±0.8
5.27	514	54	10.5	±0.9
4.85	449	62	13.8	±1.1
4.35	561	121	21.6	±1.2
3.77	315	83	26.4	±1.7
3.09	548	164	29.9	±1.3
2.74	603	203	33.7	±1.3
2.19	305	129	42.3	±1.9

has also been depicted by a graph of the log of the surviving spores plotted against the dose (Fig. 1). The data are consistent with an exponential relationship, thus supporting the single-unit action, or Treffer hypothesis, of radiation killing. In a similar type of investigation using the spores of *Aspergillus terreus*, Stapleton *et al.* (1952)

found that the survival curve obtained with X-rays was sigmoid rather than exponential. Exponential survival curves were obtained, however, as in the present investigation, with spores exposed to more densely ionizing radiations, such as neutrons and alpha particles. No obvious explanation is at hand for the seemingly contradictory conclusions indicated for the mechanism of X-ray

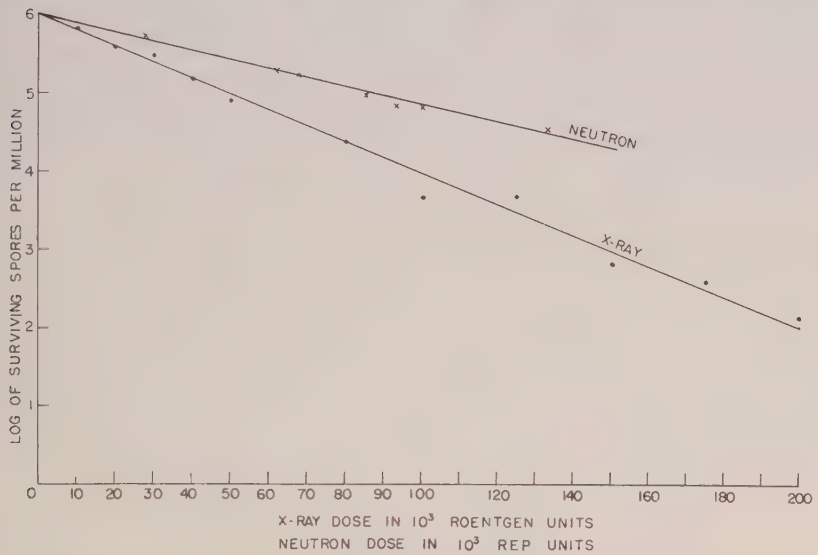

FIG. 1. Relationship between dosage of radiation (X-rays and fast neutrons) and inviability of *Glomerella* conidia. Each point represents an average of several determinations.

effects on fungus spores in these two investigations. Significant differences in X-ray sensitivity may distinguish *Glomerella* and *Aspergillus* spores, and, of course, the details of the irradiation procedures were not identical.

Aside from the shapes of the survival curves it should be noted that, at equivalent doses, the X-radiation seems considerably more lethal than the neutron radiation. This difference in killing effect is difficult to explain on the basis of the ionizing properties of the two types of radiation. Indeed, Stapleton *et al.* (1952) found that the more densely ionizing radiations were more efficient than X-rays in inactivating spores. However, as mentioned earlier, the condi-

tions under which the radiations were administered in the present investigation were not the same for neutron bombardment and for X-radiation. The X-radiation was performed on a spore suspension in distilled water over a relatively short time, whereas the neutron bombardment was performed on the intact culture tubes over a relatively long time. The greater killing effect of X-rays may there-

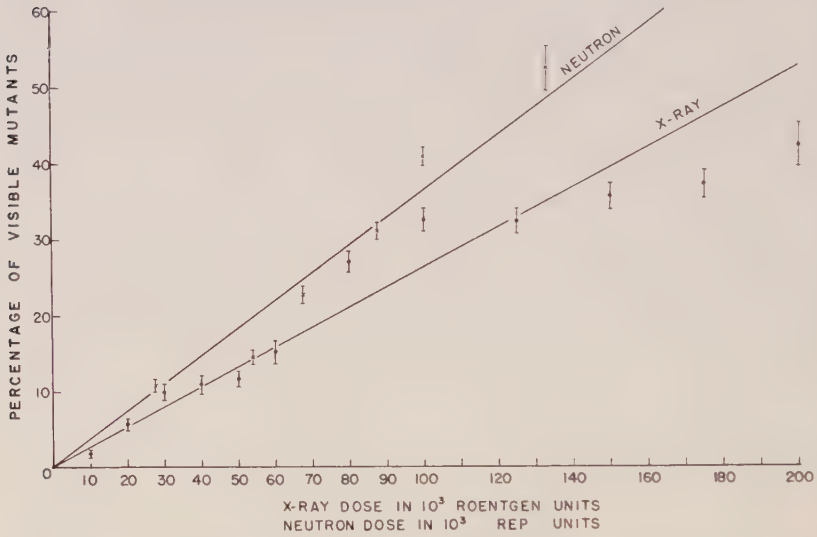

FIG. 2. Relationship between dosage of radiation (X-rays and fast neutrons) and percentage of visible mutants among the colonies produced by surviving *Glomerella* conidia.

fore be due to the conditions under which the radiation was performed rather than to the nature of the radiation itself.

When *Glomerella* spores are suspended in water, as in the X-ray treatments, they absorb water and increase in size. The approximate average volume of conidia taken from a sporulated mycelium is 256 cu. μ. After suspension in water the conidia increase to an average volume of 357 cu. μ. This absorption of water by the X-radiated spores probably rendered them more sensitive to the radiation. Stapleton and Hollaender (1952) demonstrated that *Aspergillus* spores increased considerably in radiation sensitivity after absorption of water, 99 per cent of the suspended spores being killed by only 70 per cent of the X-ray dose required to kill 99 per cent of

the dry spores. A comparable increase in radiation sensitivity of *Glomerella* spores after suspension in water would account for the apparently greater lethal effect of X-radiation as compared to neutron bombardment.

The mutagenic effect of X-radiation is shown in Figure 2. The line drawn through the points represents the average of all the points and is calculated on the assumption that the relationship between

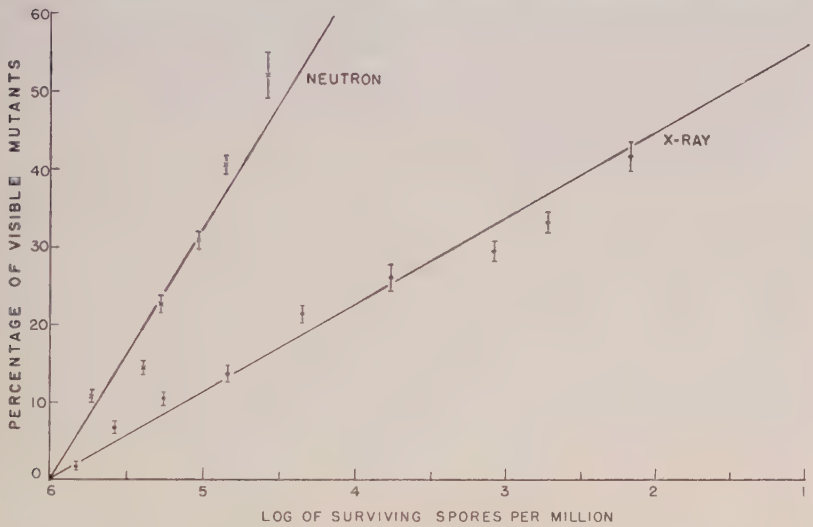

FIG. 3. Relationship between the lethal and mutagenic effects of X-radiation and neutron radiation. The points represent the percentage of visible mutants found among the fraction of spores which survived the radiation.

mutation rate and dose is linear. The manner in which the points are distributed about the line then becomes an indicator of the accuracy of the assumption of a linear relationship. At low doses a linear relationship appears to exist between the percentage of mutants and the size of the dose, but at higher doses the points are consistently too low. This falling away from simple proportionality is to be expected, since with increasing mutation rates an increasing number of mutants would represent multiple mutations, but of course would be counted only once. Some of the deviation of individual points (Fig. 2) from the straight line representing the average can be correlated with variations in killing. Thus a plot (Fig. 3) of the percentage of mutants against the log of the surviving

spores produces a distribution of points with less scatter than does the plot of the percentage of mutants against dose. Killing and mutation rates are seen to be closely correlated, and, in fact, the killing effect may be largely a manifestation of lethal mutations.

When the mutagenic effect of neutron bombardment is plotted (Fig. 2) against dose and the straight line indicating the average is drawn through the points, it is apparent that the mutagenic action of neutrons is somewhat greater than that of X-rays for equal doses. However, the significance of this difference is questionable because of uncertainty in measuring precisely the absolute dose of irradiation. On the basis of the work of Stapleton and Hollaender (1952), it would be expected that the increased water content of the spores exposed to X-radiation should have rendered them more sensitive to the mutagenic as well as to the lethal effects of the radiation. If such an increased sensitivity occurred, then, by comparison, the fast neutrons must be considerably more efficient as mutagenic agents than are X-rays. This greater mutagenicity of fast neutrons is clearly shown by a plot of the percentage of mutants against the log of the survivors. In Figure 3 it can be seen that equivalent lethal doses of fast neutrons produce more than three times as many visible mutants as do X-rays among the surviving spores. In addition, at the higher doses it is significant that the mutagenic effect of fast neutrons appears to continue as a linear function of the dose rather than to fall off as with the X-rays.

Discussion

In view of the greater role played by subjective factors in estimating mutants and the additional variables involved in transferring colonies for mutant determination, it is not surprising that the mutation data should be somewhat more variable than the data concerned with lethal effects. Most of the colonies recorded as mutant at low doses are undoubtedly the result of single genetic changes. In fact, nearly all the mutants so far tested genetically have been shown to be due to changes at a single locus, although a few double mutants have been obtained at higher doses.

Measurements of lethality may also be measurements of gene changes lethal changes, of course, as contrasted with the viable visible changes usually recorded as mutations. The assumption that

loss of viability in a spore after irradiation is due to lethal mutation is especially germane to the Treffer hypothesis, or target theory, of killing by radiation. The shape of the survival and mutation curves after treatment of spores by X-rays and neutrons in this and in many other investigations indicates a single-unit type of action for these radiations. On the basis of a single-unit action it becomes possible to calculate the sensitive volume in which the action occurs. Although equating of this sensitive volume with the volume of genes

TABLE IV

DATA RELEVANT TO THE TARGET THEORY OF RADIATION EFFECTS

Radiation	Biological effect	37 per cent dose	No. of targets ("genes" 5 mμ in diameter)	Radiation-sensitive volume (cu. mμ)
X-ray	Lethal mutation	22,000 r	700	45,800
X-ray	Viable mutation	380,000 r	40	2,600
X-ray	Mutation	15,000,000 r	1	65
Neutron	Lethal mutation	39,000 rep	500	32,700
Neutron	Viable mutation	270,000 rep	70	4,600
Neutron	Mutation	20,000,000 rep	1	65

is undoubtedly an oversimplification (see Muller, 1950, 1954, for critical discussion), nevertheless, useful information can be extracted from calculations based on target theory if interpretations are made with caution (see Lea, 1947, for discussion of target theory). Table IV records the data derived from this investigation which are relevant to target theory. The relationship between target diameter and the 37 per cent dose was determined by reference to the graphs in Lea (1947). The 37 per cent dose corresponds to an average of one hit per target.

According to target theory as related to a multiplicity of targets, where there are n targets of a given radius, a 37 per cent dose will be 1/n times as large as if there were only one target of the same radius. If the plausible assumption is made that the diameter of a

gene is about 5 mμ (Catcheside, 1948), then the 37 per cent dose with X-rays for such a target is 15×10^6 r (Lea, 1947). The 37 per cent dose obtained for killing by X-rays in this investigation, where a multiplicity of targets certainly exists, was found to be 22,000 r (Table IV). Therefore the number of targets of gene size (5 mμ), ionization in any one of which can produce a lethal effect, must be about 700 (15×10^6 divided by 22×10^3).

Similar calculations based on the 37 per cent dose for killing by neutrons indicate about 500 targets. This figure is probably too low in view of the resistant characteristics of the relatively dry spores exposed to fast neutrons. If the targets represent genes which may be mutated to a lethal form, then *Glomerella* must have, roughly, about 1,000 such genes. This number of genes for *Glomerella* seems reasonable, and, when the relatively simple characteristics of *Glomerella* are considered, it is in accord with estimates of the number of genes in other organisms (Gowen and Gay, 1933; Bridges, 1935; Spuhler, 1948).

The 37 per cent doses may, of course, also be determined for visible mutation by X-rays or by neutrons. However, the number of targets obtained by calculation from such mutation data is difficult to interpret. The number of targets for visible mutation by X-rays is about 40 and for neutrons about 70. These numbers might imply that *Glomerella* contains fewer than 100 genes capable of showing visible mutation. However, several hundred visible mutants of *Glomerella* have already been recorded during the course of this investigation, and it is implausible to attribute these mutants to changes at fewer than 100 loci. In any event, lethal mutation and viable mutation are not properties respectively of two different sets of genes. Whether a gene change is lethal is largely dependent upon the environment of the organism in which the change is effective. The commonly obtained growth-factor mutants of *Glomerella* are lethal on a minimal medium, but entirely viable and visibly mutant on a complete medium. Doubtless many additional lethal changes could be transferred to the viable-mutant category if an appropriate environment were provided for the growth of the mutant spores. It seems most reasonable, then, to explain the number of targets found for visible mutation (40 or 70) by assuming that an ionization in any one of many different genes may produce either a

lethal or a viable visible change; the ratio of the probability of a lethal to a viable change would then be of the order of 700 to 40 for X-rays and 500 to 70 for neutrons. Thus, after X-radiation, lethal changes are nearly twenty times as numerous as visible viable changes, and after neutron bombardment, about seven times as numerous. These ratios further suggest that ionizations are very crude tools for modifying genes, since complete destruction of the vital activity of a gene appears far more probable than a simple remodeling which would leave the vital activity of the gene modified but functional.

A contrasting point of view is contained in Muller's (1950) estimate that in *Drosophila* the total mutation frequency is five times as high as the frequency of lethals. If a similar proportion exists in *Glomerella*, then one must assume that the overwhelming majority of gene changes produce no visible effect, which is, of course, quite possible. It seems reasonable to assume that the proportion of mutant genes with visible effects in any organism should be largely dependent upon the complexity of the organism. A simple organism like *Glomerella* offers fewer opportunities for visible genetic changes than does a complex organism like *Drosophila*.

The target theory of radiation killing leads to the conclusion that only a minute fraction of the volume of a cell is critical in the response to radiation. *Glomerella* conidia have an average volume of about 300 cu. μ, with a nuclear volume of less than 10 cu. μ. Thus the sensitive volume for killing (about 50,000 cu. mμ) occupies less than one six-millionth of the total spore or about one two-hundred-thousandth of the nucleus.

Summary

1. The fungus *Glomerella* has biological characteristics which make it a suitable laboratory tool for measuring the mutagenic and lethal effects of ionizing radiations over a dosage range of 10,000 r to 200,000 r.

2. Results of X-ray and of fast-neutron radiation of *Glomerella* conidia support the target theory of radiation killing and indicate that in *Glomerella* there are about 1,000 genes in which a single ionizing particle can produce a lethal change.

3. Calculations based on target theory suggest that the proba-

bility of ionization in a gene producing a lethal change instead of a viable visible change is nearly 20 to 1 with X-rays and about 7 to 1 with neutrons.

4. A comparison of the mutagenic and lethal effects of fast-neutron bombardment and of X-radiation shows that, for doses of equal lethal effect, the neutron radiation produces more than three times as many viable visible mutants as does X-radiation.

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FORESTRY

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EFFECTS OF INITIAL SPACING ON THE DEVELOPMENT OF YOUNG JACK PINE IN NORTHERN LOWER MICHIGAN

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The growth and development of young forest stands are influenced by a number of environmental conditions. Of these, stand density is perhaps the easiest to control. Established stands can be thinned to desired densities, and the initial spacing of plantations can be controlled when the trees are planted.

In order to learn more about desirable initial stand density for jack-pine plantations in lower Michigan, the Lake States Forest Experiment Station established a spacing study on the Manistee National Forest near Wellston, Michigan, in 1941. The ten-year results were reported by Rudolf (2). The present paper, based on observations made in 1954, reports the fifteen-year results.

The Experiment

The area studied is a ten-acre planting block divided into twenty-five square plots 0.4 acre in size. The plots were planted with 1–0 jack pine of local-seed origin at five spacings—$1\frac{1}{2} \times 1\frac{1}{2}$, 3×3, 5×5, 7×7, and 9×9 feet. Each of the five spacings was replicated five times, in the form of a Latin square.

The planting site was a level, abandoned field, with soil classed as Grayling sand and typical of the poorer sandy soils planted to jack pine in northern lower Michigan. The ground cover consisted primarily of grasses, sedges, and sweet fern.

Before the planting, the scattered oak and cherry saplings were cut. The jack pine was then planted by hand with a planting bar, in freshly prepared scalps where the ground cover had been cleared away with a mattock.

Initial Results

At the end of the first growing season survival averaged 77 per cent. All fail spots were replanted with 2–0 jack pine to keep the density consistent with the objectives of the study. Planting losses the second year were negligible, and no further replanting was done.

The third year after planting, in 1943, when the jack pine were four years of age from seed, survival ranged from 90 to 93 per cent. The mortality was caused by the red-headed pine sawfly, pine-oak gall rust, grasshoppers, and competition from sprout growth. The height of the jack pine at the different spacings varied from 1.8 to 2.0 feet.

Ten-Year Results

In 1949, when the trees were ten years of age from seed, Rudolf (2) found survival to range from 87 to 91 per cent and average heights from 8.4 to 8.8 feet among the various spacings tested. These differences in survival and height were not significant, showing no apparent effect due to spacing.

Differences in diameter growth, on the other hand, had become quite apparent. Average diameter breast high ranged from 0.7 inch for the closest spacing ($1\frac{1}{2} \times 1\frac{1}{2}$ feet) to 1.3 inches for the widest (9×9 feet). An analysis of regression showed the trend of diameter growth in relation to spacing to be highly significant. When the average diameters for the individual spacings were compared, those of trees in the $1\frac{1}{2} \times 1\frac{1}{2}$ foot plantings proved to be significantly smaller than those of trees in the other spacings. The average diameter in the 3×3 foot plantings was also significantly smaller than that in the 9×9 foot ones. The differences in average diameter growth among the wider spacings were not significant at ten years.

Fifteen-Year Results

In 1954, when the trees were fifteen years old from seed, the effects of spacing were more pronounced (see Table I).

General condition of stands

Survival in the $1\frac{1}{2} \times 1\frac{1}{2}$ foot spacing dropped from 88 per cent in 1949 to 69 per cent in 1954, most of the losses being caused by

suppression or girdling injuries by snowshoe hares. All of the trees are spindly. The crown-class differentiation evident in 1949 is now masked by the very crowded condition of the stand. The lower branches are dead to a height of about eight feet, and the original ground cover has been shaded out. Nearly all of the trees have been attacked by the white-pine weevil, but most of the main stems are straight.

Survival in the 3 × 3 foot spacing is now 80 per cent compared to 88 per cent in 1949. The remaining trees are well differentiated into crown classes. About 10 per cent are badly suppressed and will

TABLE I

EFFECT OF STAND DENSITY ON THE GROWTH OF YOUNG JACK PINE AT AGE TEN AND AGE FIFTEEN

Original spacing, in feet	No. of trees planted per acre	At age 10 years		At age 15 years	
		Average d.b.h., in inches	Average height, in feet	Average d.b.h., in inches	Average height, in feet
1½ × 1½	19,360	0.7	8.4	1.0	13.0
3 × 3	4,840	1.1	8.8	1.8	14.7
5 × 5	1,740	1.2	8.7	2.3	14.9
7 × 7	890	1.2	8.4	2.8	15.9
9 × 9	540	1.3	8.5	2.8	14.8

soon drop out of the stand. The lower branches of all trees are dead to a height of about six feet, and the original ground cover is largely shaded out. Most of the trees have straight stems despite the extensive weevil damage.

The losses since 1949 in the 5 × 5 foot spacing have been negligible. The trees show good crown-class differentiation, with only 5 per cent suppressed. The live crowns reach to within about four feet of the ground, and traces of the original ground cover still persist. Weevil damage has caused a few of the trees to fork, but most are straight-stemmed.

Survival in the 7 × 7 foot spacing has not changed since 1949. The branches of the trees are now interlaced, and crown-class differentiation is beginning. Very few of the trees can be classed as suppressed or even as intermediate. Nearly all of the lower branches

are alive, and most of the original ground cover of grasses and sedges is still present. Although a larger proportion of trees are forked than in the 5 × 5 foot spacing, there are enough straight ones to produce a good stand.

Survival in the 9 × 9 foot spacing has not changed since 1949. The trees are still growing as individuals, with no crown-class differentiation. The branches are just beginning to touch, and the live crowns still reach the ground. Many of the lower branches are nearly one inch in diameter and may be expected to persist for some time.

DIAMETER GROWTH

The effects of spacing on the average tree diameter were much more noticeable in 1954 than in 1949. The trend of increasing diameters with wider spacing is shown in Table I. The differences in the average diameters for the individual spacings are now obvious except between the 7 × 7 foot and the 9 × 9 foot plantings. However, the crown differentiation which is beginning in the 7 × 7 foot spacing indicates that the trees are now fully utilizing their growing space. Those in the lower crown classes will probably show a reduction of diameter growth in the 1959 remeasurements.

In the closer plantings the lag in diameter growth is most marked in trees with lower crown classes, but the effects also appear in the growth of the dominant trees. The average diameters of the dominant trees in the 1½ × 1½, 3 × 3, and 5 × 5 foot spacings are 1.8, 2.2, and 2.6 inches, respectively, compared to 2.8 inches in the 7 × 7 foot and the 9 × 9 foot spacings.

HEIGHT GROWTH

In contrast to the effects of spacing on diameter growth, only the trees spaced 1½ × 1½ feet show a significant depression in average height (Table I). The small differences in the average height of the trees in the wider spacings do not indicate any trend than can be attributed to spacing. The slackening of height growth in the 1½ × 1½ foot plantings is confined to the lower crown classes; the dominant trees are as tall as the trees in the 9 × 9 foot spacing.

Discussion

It is now possible to draw some tentative conclusions as to the effect of stand density on the growth of jack pine. Obviously, both

the 1½ × 1½ foot and the 3 × 3 foot spacings are too dense to permit commercial thinning before the diameter growth of the dominant trees has been seriously impaired. If a noncommercial thinning is not made soon, commercial ones may never be possible. One advantage of these close plantings, however, is that early crown closure will shade out the ground cover and reduce the chance of spittle-bug infestation. The close spacings also provide better conditions for rabbits, as evidenced by the girdling of trees in the stands with the 1½ × 1½ foot spacing.

The dominant trees in the 5 × 5 foot spacing are growing nearly as fast in diameter as those in the 7 × 7 foot and the 9 × 9 foot spacings. The trees planted at 5 × 5 foot intervals are crowded enough to prevent the formation of heavy limbs. The expected slowdown in diameter growth may be offset by the smaller knots and the denser wood produced. Another study (1) indicates that jack pine spaced 5 × 5 feet will require a thinning that is not commercially practicable for pulpwood. If a market can be developed, trees too small for pulpwood could be sold for fence posts, making the first thinning a commercial operation. The 5 × 5 foot spacing is the maximum stand density for satisfactory development of the stand.

The 7 × 7 foot spacing is the minimum stand density for satisfactory development of the trees. Although the limbs are heavier and the trees of poorer form than those in the 5 × 5 foot planting, natural pruning and bole form may improve as the stands close in. No thinning will be needed until they are about thirty years old, when a commercial thinning can be made. The trees spaced 9 feet apart are too heavy-limbed to yield good saw timber or acceptable pulpwood on a short rotation.

Summary

A study of jack-pine spacing, begun in 1941 on the Manistee National Forest in lower Michigan, demonstrates the effects of stand density on the early growth of jack pine. In 1954, at fifteen years from seed, diameter growth of the dominant trees had been seriously impaired in plantations spaced 1½ × 1½ feet and 3 × 3 feet. Height growth of the dominant trees had not been affected by stand density. Plantations spaced 5 × 5 feet are developing satisfactorily now, but will need thinning before a commercial thin-

ning is practicable. Thinnings in plantations spaced 7 × 7 feet can be deferred until a commercial thinning is possible. Plantations spaced 9 × 9 feet are too sparsely planted for satisfactory development of the stand.

LITERATURE CITED

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